Frequency dependent pollination: nonlinear relationship consistent in field and model data

Helen Czioska

Supervisor: Dr. Gita Benadi, Department of Biometry and Environmental System Analysis
Co-supervisor: Prof. Dr. Alexandra-Maria Klein, Department of Nature Conservation and Landscape Ecology

Freiburg, 2015

possible titles
should contain:

- Frequency dependence (negative frequency dependence), frequency dependent pollination, frequency dependent selection

- model /agent-based model/ simulation/ foraging model /model data

- natural field condition/ field data/ natural condition /

- drivers, reasons, explanation, consistent, coincide, causes, depend, understand

- co-flowering plants

- non-linear, sigmoid, cubic,

ideas...

- Understand frequency dependence: Results consistent in natural field conditions and agent-based modeling

- Reasons for positive and negative frequency dependent selection

- Drivers of Frequency Dependent Pollination in natural field condition and agent-based modeling

- Frequency Dependence in natural field conditions and agent-based modeling

- Flower frequency dependence of pollination

- Spatial distribution and cover as limited drivers of flower frequency dependence

- Frequency dependent pollination of co-flowering plants

- possible causes for frequency dependent pollination of co-flowering plants

- Natural conditions and simulation experiment coincide in negative frequency dependence

- Negative frequency dependence coincide in natural conditions and simulation experiment

- Sigmoidal frequency dependence coincide in natural field condition and foraging model

- Sigmoidal frequency dependence consistent in natural field condition and foraging model

- Nonlinear Relation of Pollinator Visitation to Flower Frequency

- Field data and foraging model show sigmoidal frequency dependence

- Comparing field with model data: Frequency dependence appears to be non-linear

- Frequency dependent foraging might be non-linear

- Frequency dependent pollination: nonlinear relationship consistent in field and model data
  foraging model agent-based model simulation

1 Introduction

Storyline

- biodiversity loss /important to maintain and understand

- what are the divers for biodiversity?

- pollinator loss, have to understand underlying rules/drivers/

- pollination crucial for most plants (self-incompatible)

- Interspecific and intraspecific competition

- pollinator service shared ressource of coflowering plants

- increased forager activity and attractiveness can respond in higher fitness

- response of pollinators to certain variables like density, frequency, traits got a lot of attention over the last 2 decades since pollinator decline

- complex multidimensional interactions

- other factors: presence/absence of similar flowering species, spatial scale

- detects bits and peaces to get a greater understanding

- The effect on density is rather well studied

  Science agrees on a form of density dependence for pollination success from various studies with lab, field and modelling approaches:

  (Bernhardt et al., 2008) field (Elliott and Irwin, 2009) field (Essenberg, 2012) numerical Model and field (Kunin, 1997) field (Kunin, 1993) experimental (Morris et al., 2010) model, field (Rands and Whitney, 2010) model (Stout et al., 1998) lab

  usually positive

  Frequency-dependence (FD) of survival or reproduction occurs when the relative fitness of a species changes as a function of its frequency in the community.

  According to ecological theory, frequency dependent pollination could have far-ranging consequences for species coexistence and the maintenance of diversity: While negative frequency dependence (i.e., preferential pollination of rare flower types) is thought to increase diversity, positive frequency dependence (higher pollination success for common flower types) tends to reduce diversity in modeling studies (May 1974, but see Bever 1999, Molofsky and Bever 2002).

  +FDP - fixation on one phenotype for color morphs of one species - possible reduction of diversity (rare flowers do not get enough pollination, reproduction disadvantage) see Molofsky and Bever 2002 - the most frequent species is becomming even more frequent

  resons/explanations: - search image hypothesis (sensory system becomes trained, minimize search times) - search rate hypothesis (tradeoff search time and probability to find the next rewarding flower)

  -FDS - promotes phenotye diversity - can promote landscape diversity - known for non-rewarding flowers

  reasons: - if a species is rare enough, the negative experience is not stored long enough in the short term memory and it gets exploratory vistits by the pollinator

  For animal-pollinated plant species, optimal foraging theory predicts that under most circumstances pollinators should favor common flower types over rarer ones (Kunin and Iwasa, 1996) , but so far this has rarely been tested.

Research: Most previous studies of frequency-dependent pollination focused on within-species variation in pollination success of different flower color morphs in the field or in the lab with a "bee-board" with corolla color as differing flower trait.

In the review of Smithson 2001 11 of 13 lab experiments showed a significant FD. Bumblebees tend to visit the common morph if rewarding and the rare morph if unrewarding (for simple and controlled conditions for color morphs). Lab easy o get clear colors and equal rewards for all color morphs.

(Smithson and Macnair, 1996) (Smithson and MacNair, 1997)

Not so clear for field experiments. Mostly just trends without significance (for both negative and positive FDS)

Eckhart et al. 2006 Epperson and Clegg 1987 Gigord et al. 2001, Jones 1996

In the review by Smithson (2001), 11 of 13 lab experiments using artificial flowers on a "bee-board" with rewarding flowers showed significant results for frequency dependence. 10 of those were done with rewarding flowers and resulted in positive frequency dependence. The only experiment resulting in negative frequency dependence was done with non-rewarding flowers (Smithson and MacNair, 1997). The few field experiments on frequency dependence concentrate on color morphs and are not consistent. While Epperson and Clegg (1987) found the rare white morph of *Ipomoea purpurea* to be undervisited (but not the colored morphs), Eckhart et al. (2006) was the first to prove negative frequency dependence for a rewarding species (*C. xantiana ssp. xantiana*). Other experiments had no significant results (eg. Jones 1996) and experiments on natural flower communities lack completely to our knowledge.

rarely been addressed: FD of certain species within a floral community (in contrast to flower morphs)

been considered in the context of frequency dependence.

new because: -never been a comparison model and field data for fd -non-linear relationship (consistent) -findings in the field - most models see how pollinators can maximize their income, not view of the plant (KI, Song 2014)

quantity and quality: Pollen must be from the right plant. Problem for scarce plants.

Research Questions

In this study I want to address the following questions:

1. Does the per-flower pollinator visitation change with the frequency of the flower in a floral community?

2. What kind of a frequency dependent relationship can be found? (linear, positive, negative, saturated, hump shaped, sigmoid)

3. Are there drivers for frequency dependence? (e.g. flower cover, species richness, similarity index, degree of clustering, forager behavior)

In this thesis, I tested the existence of FD within a gradient of frequencies of five flowering plant species within a grassland plant community on the area of the Jena Experiment. To explore the deeper drivers of FD I developed a spatially explicit Agent-Based Model (ABM). The autonomous agents respond with set foraging behavior rules to changing frequency and clustering values for the two co-flowering plant species. The results of the model were compared to field data.

2 Natural Field Condition

2.1 Methods

Study Site

The data used in this analysis were collected in the area of the Jena-Experiment, locatednorth of the city of Jena in the middle of Germany (N50°55′ E11°35′ ; 130 m a.s.l.). Mean annual temperature is $9.3°$C and mean annual precipitation 578mm (Kluge et al., 2000). In 2002, 10ha of strongly fertilized arable field in a floodplain of the Saale river were converted into a biodiversity experiment. Species mixes of 1, 2, 4, 6, 8, 16 and 60 species from a pool of 60 common European grassland species were sown in 82 plots a 20m x 20m (Roscher et al., 2004).

The Jena Experiment has the purpose to explore the effect of plant diversity (species richness and functional group richness) in grassland communities and is object to numerous studies and experiments. The plots of the Jena Experiment are mowed twice a year in accord to standard grassland management. Parts of each plot are additionally weeded twice a year to maintain the original plant composition. Two subplots were excluded from the weeding since 2002 ("Old Invasion Plots", 4m x 5.5m , 22m^2) and since 2009 ("New Invasion Plots", 5m x 3.5m, 17.5m^2) to evaluate invasive potential and effects. Subplots with continuous weeding were scarce with flowers and had a generally low species richness. Hence I collected the data in the old and new invasion plots with a higher cover, species richness and diversity. From the 82 plots of the Jena Experiment I only included plots with a floral cover between 20% and 70% for better comparison. In total, 23 plots were sampled throughout this study.

The Sampling

I selected the focal plant species during the field work as the flora changed very quickly. A focal species had to be flowering for at least one week in the sampling time and be present in at least five plots with a differing frequency to get sufficient data. Therefore, I chose *Lathyrus pratensis*, *Lathyrus pratensis*, *Trifolium pratense* and *Onobrychis viciifolia* of the family Fabaceae and *Geranium pratense* of the family Geraniaceae (Supplementary material, tab. S1).

Pollinator observations were only made during suitable weather conditions (maximum partly overcast, maximum light wind, min. $15°$C). The sampling took place between 9am and 5pm. Overall, 15 days between 20th of July and 12th of August 2014 were suitable for pollinator observations.

Per observation I recorded all pollinator activity during 15 minutes in a 80cm x 80cm subplot. This size is feasible to watch even with high pollinator activity and floral cover. The documentation included all visits to flowers of the focal plant species and accumulated visitation number for all other flowers in the subplot. I counted the flowers of the focal species to calculate the per-flower visitation rate. As possible drivers for visitation rate changes, I estimated the floral cover and identified all other flowering plant species present on subplot and plot level. Each plot contained eight evenly distributed subplots for 2h observation time per focal species and frequency.

Statistical Analysis

Per-flower visitation rate is a effective response variable for analyzing the effect of frequency dependence. It is calculated as followed:

$$VR_i = \frac{\Sigma V_i}{\Sigma F_i}$$

With VR_i being the per-flower visitation rate of species i, V_i the count of all visits to a flower with species i within 15 minutes and F_i a flower of species i within the subplot. Therefore, the response variable is no count data and was treated with a Gaussian error distribution in the analysis.

The explanatory variables of the beyond optimal model include species richness, floral cover and frequency as single, quadratic and cubic term with and without interaction with species, all on the plot level and as continuous variable. Species was included as nominal response variable. All statistical analysis was performed with R, version 3.1.2. (R Core Team, 2014).

I used variance inflation factors (VIF) to check weather any variables in the dataset are collinear and should be removed prior to the analysis. With all values below two, there was no sign for collinearity and therefore OK to use them in the model selection as explanatory variables (Zuur et al. 2007, supplementary material, tab. S2). Pairwise scatterplots with included correlation of coefficients also showed only minor correlation (Supplementary material, fig. S2).

The sampling design contained 8 observations per plot summing up to 2h of observations per species and frequency. Therefore, the data are not independent and I chose a linear mixed effect model with subplot nested in plot as random effect. I used the function "lme" from the R package "nlme" (Pinheiro et al., 2014) for all further analysis. The mixed effect model was significantly better compared to a generalized least squares model with the same set of explanatory variables (models estimated with REML, L = 8.96 , df =2 , P = 0.01).

The beyond optimal model with the full set of reasonable predictors and interactions showed a strong pattern of heteroscedasticity in the residuals. With the varIdent-function from the R-package "nlme", every species is allowed to have its own variance structure and we can maintain the differences in attractiveness of the five focal species in the model as biological information. The weighting provided a significantly better variance structure for the model (L = 401.48, df = 4, $p < 0.0001$).

I performed a backward stepwise deletion of interactions and predictors with maximum likelihood estimation (ML) for each model. The loss of explanatory power in the model after removal of a variable was tested by comparing the Akaike information criterion (AIC) of the model with and without the explanatory variable (ANOVA model comparison). If there was no significant loss of explanatory power, the variable was removed. The selection was verified by a global selection via the dredge-function from the R-package "MuMin" (Barton, 2014) with maximum likelihood estimation.

The final model was again validated by plotting the normalized residuals against fitted values. The vertical gap in the residuals can be explained by the difference in flower attractiveness. *Geranium pratense* and *Onobrychis viciifolia* got very high visitation rates whereas *Trifolium pratense*, *Lotus corniculatus* and *Lathyrus pratensis* had generally only few visits. However, the heteroscedasticity of residuals could be dealt with by the weighting and the mean of the residuals is close to zero (< 0.0001, supplementary material fig. S3).

2.2 Results

Visitation Rates

In total, I made 385 observations, each represents pollinator activity records for 15min in a 80cm x 80cm plot. Accumulated, I analyzed data from 96,25h of observation on 246.4m^2.

Onobrychis viciifolia was the most attractive plant with a maximum of 318 visits in one observation. The per-flower visitation rate (counted visits to all flowers divided through the number of flowers of the focal plant species in the subplot) varied strongly with the attractiveness of the focal species. Per observation, I recorded 1.4 ± 1.8 ($\pm$ SD) visits per flower with a maximum of 10.7 visits per flower (again *Onobrychis viciifolia*) and 31 observation with no visit at all to the focal species. The per-flower visitation rate was significantly different between the two very attractive species *Geranium pratense* and *Onobrychis viciifolia* and the three less attractive species *Trifolium pratense*, *Lotus corniculatus* and *Lathyrus pratensis* ($P \leq 0.001$, tab. **??**). The subplots contained 3 ± 1.2 ($\pm$ SD) flowering species including the focal species, the species richness was higher on plot level with 8 ± 2.4 ($\pm$ SD) flowering species.

Frequency Dependence

Floral cover and species richness had both individually and in the interaction term with frequency no effect on the visitation rate and were removed from the model (Cover: $F_{df=1} = 1.17$, $P = 0.28$; Species Richness: $F_{df=1} = 1.15$, $P = 0.29$).

The linear mixed effect model shows an effect of species and frequency individually and with interactions on the per-flower visitation rate (Species: $F_{df=4} = 141.13$, $P \leq 0.0001$; Frequency: $F_{df=1} = 18.29$, $P \leq 0.0001$; Species x Frequency $F_{df=4} = 5.2$, $P \leq 0.001$, tab. **??**). Interestingly, frequency contributes also as quadratic and cubic term with its interactions to species explanatory power to the model, giving the relationship a non-linear character (Tab. **??**).

Figure **??** shows the third degree polynomial relationship of all focal species and the summed data except *Lathyrus pratensis* which has a quadratic relationship. The sigmoid curve is defined by a strong increase for frequencies below 20% followed by a minimum between 50 and 80% depending on the species before raising again with increasing dominance of the focal species. However, the visitation rate of *Lathyrus pratensis* presents a maximum at 60% frequency and decreases afterwards.

3 Agent-Based Foraging Model

3.1 Methods

Agent-Based Models ("ABM", also known as Individual-Based Models "IBM") are a valuable tool for assessing interactions in dynamic networks like financial markets, game theory, spread of diseases or, like this case, ecosystems. The model contains multiple agents which behave independently after given behavior rules and are able to interact with the environment and each other. Agent-based models are especially suitable for analyzing behavior shifts with changing environmental conditions (eg. nectar reward or flower quantity).

ABMs got important and popular throughout various research areas including ecology and evolutionary biology (DeAngelis and Mooij, 2005). Also foraging models grew in number over the last years addressing a broad range of research questions. Dornhaus et al. (2006) looked at the benefits of a recruitment system and colony sizes. Faruq et al. (2013) compared the foraging success while applying different flower colors by varying the wavelengths over time. Bukovac et al. (2013) simulated the difference between the parallel visual scan of honey bees and the serial visual scan of bumble bees to for the ability to avoid distractions during foraging. The ABM of Hanoteaux et al. (2013) showed reproduction success of plants with unequal attraction to the pollinator.

The combination of an ABM with experimental data is a rare but promising approach. The fist to apply this method in foraging models was Dyer et al. (2014). They trained honey bees in a lab experiment to fine color discrimination to check for their flexibility to change when the reward changes between flower types. Afterwards, Dyer et al. (2014) confirmed the findings with a ABM.

I used NetLogo (Wilensky, 1999) as programming environment. It is a simple but powerful tool for making ABMs and connectible with R through the R-package "RNetLogo" (Thiele et al., 2012).

Assumptions

The model was developed on empirical findings for foraging rules and pollinator behavior. It is a simple spatial model of two co-flowering plant species competing over pollination service.

In the model, all pollinators (from now on called "bee-agents") are identical and the two flower types only differ in their initial species identity. Reward regrowth, handling times to extract the reward and its attractiveness towards the bee-agents is identical for both species. Corolla color is only assigned for better visualization and is not important for the model or the bee-agents, respectively. All bee-agents behave under the theory of flower constancy which is empirically tested and proven for various pollinators (e.g. HILL et al. (1997) for hones bees, Chittka et al. (1997) for bumble bees, Goulson and Wright (1998) for hoverflies and Goulson et al. (1997) for the butterfly *Thymelicus flavus*).Flower constancy is the tendency of a pollinator to keep visiting the same flower species instead switching to more rewarding or closer species (Chittka et al., 1999; Waser, 1986). Because we are interested in the visitation rate of flowers in different frequencies, the energetic costs and the limit of gained rewards of the bee-agents are ignored. Furthermore, they do not communicate and always empty a flower completely.

Model Environment

In NetLogo, the "world" is a spatial grid with a set number of cells called patches. Agents are not spatially explicit and can move freely over the patches according to their given behavior rules. Patches and agents both have own properties and can interact with each other. In my model, the "meadow" has 100x100 grid cells with horizontally and vertically wrapping to avoid edge effects. Every grid cell can either contain a single flower of one of the two species or grass. The flowers are randomly distributed over the meadow. Figure 1 gives a set of exemplary model environments with changing environmental conditions. Floral cover is defined as the percentage of the patches being flowers and the cluster number equals the average number of flowers within a flower agglomeration. Cluster can vary in the amount of flowers and shape to create a more natural meadow.

Every flower contains 1 Joule of reward in the beginning of each simulation run. The bee-agents are randomly distributed over the modeling environment, no hive is assigned and start without a fixed preference

for a flower type but just pick the closest one when the simulation starts. Every tick in NetLogo equals one second.

Behavior Rules

All bee-agents act independently from each other after given foraging behavior shown in Figure 2 (Overview of all parameters used for the model with its default settings in the supplementary material in tab. S4).

As mentioned in the assumptions, the behavior of the bee-agents is strongly influences by the theory of flower constancy (e.g. Bobisud and Neuhaus, 1975; Chittka et al., 1997; Thomson, 1981; Chittka et al., 1999; Goulson, 1994, 1999). Bee-agents are always in favor of one of the two flowering species and forage exclusively on this species. The preference can change due to lack of searching success and a series of low rewards of the preferred flower (Chittka et al., 1997). Pollinators avoid recently visited flowers (Goulson, 1999). Every bee-agent is equipped with a memory to remember the location of the last four already visited flowers (Goulson, 2000). The bee-agent can either search for a flower or visit one.

Search

If there is any preferred and unvisited flower in sight, the searching bee-agent moves on direct way towards the flower, otherwise it continues searching.

Previous research on the speed of foraging pollinators by Essenberg (2012) and Kunin (1991) (in Kunin and Iwasa 1996) gives 0.1m/sec as benchmark. Sequentially, bee-agents can move as fast as 1 grid cell per tick in this model. The vision of pollinators was studied in various experiments using a Y-maze apparatus (Dyer et al., 2008; Wertlen et al., 2008; Ne'eman and Kevan, 2001). Every bee-agent can detect flowers from a distance of 0.7m with an equivalent of 6 grid cells. The vision is reduced to a 180° cone-shaped field to the front of the agent. Pollinators tend to keep their direction while foraging (Waddington, 1980). In the model, I used a correlated random walk (CRW) to achieve a relatively natural movement (Bartumeus et al., 2005; Codling et al., 2008; Pyke and Cartar, 1992; Viswanathan et al., 2008). Empirical studies have shown a higher probability to abandon the original flower preference the longer the search remains unsuccessful (Chittka et al., 1997). If the bee-agent searches for 5 seconds (= 5 ticks) without finding any preferred and unvisited flower, the likelihood of changing its preference increases by 10% with every additional tick.

Visit and Reward Intake

When a bee-agent encounters a preferred and unvisited flower it takes up all its reward. The maximal reward a flower can contain is 1 Joule and refills each tick by a linear function ("reward-function", see tab. S4). The handling time involves three components: a time proportional to the amount of taken reward, a reward-independent constant and a skill factor (Kunin and Iwasa, 1996). In my model, a bee-agent requires 4 seconds to extract one Joule of reward plus a reward-independent handling time of 0.5 seconds. When the bee-agent just changed its flower preference it gets a 3 second penalty for inexperience (Roubik 1992 in Kunin and Iwasa 1996).

The reward taken is stored in the agent-own reward-memory. Every agent can remember the last four receives rewards. When visiting a flower, the bee-agent compares this memory with the current reward quantity. If the reward is less than half the average in the memory, the likelihood to abandon flower constancy and visit another species next increases by 10%. If the reward is exceptionally good (double of there remembered average), the change probability is set to zero (Chittka et al., 1997; Keasar et al., 1996).

The maximal number of visits within a successful pollination is possible is determined by the pollen-carryover parameter and can have a value between 1 and 16. The lower the value the stronger the heterospecific pollen interference (Campbell 1986; Benadi et al. 2012, Montgomery 2009).

After reward-collection is completed, the bee-agent updates its flower-memory and its reward-memory and continues foraging. Each visit and successful pollination is recorded for later analysis.

Simulation experiments

Parameters altered in the main analysis are frequency, floral cover, degree of clustering and pollen-carryover rate. Each parameter-combination was run 20 times with a length of 1000 ticks each (110,400 runs in total). Additionally, I performed a sensitivity analysis with parameters which can change the behavior of the bee-agents to understand drivers of the model. Table 1 presents the definition and value range of the parameters.
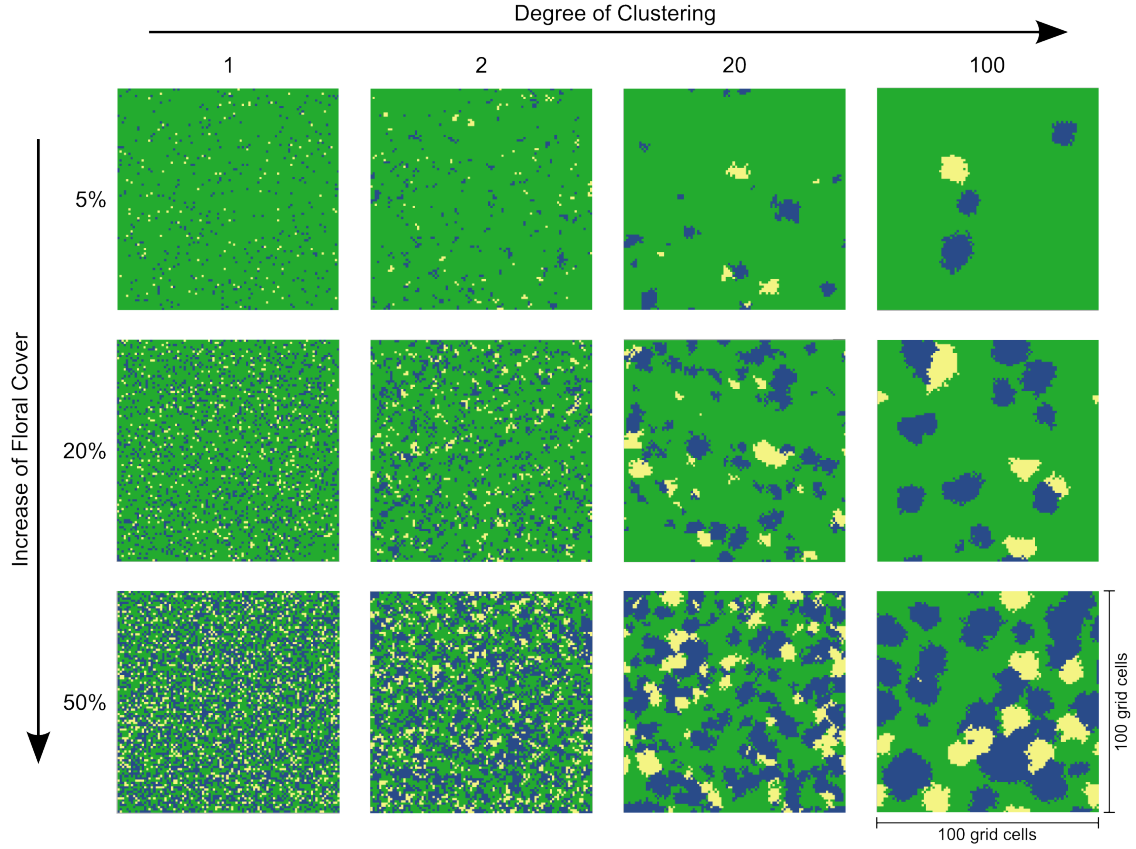

Figure 1: Exemplary model environment setups with increasing floral cover and degree of clustering. The cover expresses the percentage of patches containing a flower ($\Sigma_{patches}$ = 10 000). The cluster number equals the average amount of flowers per cluster. Flowers are randomly assigned to the clusters to achieve a more natural, uneven distribution.
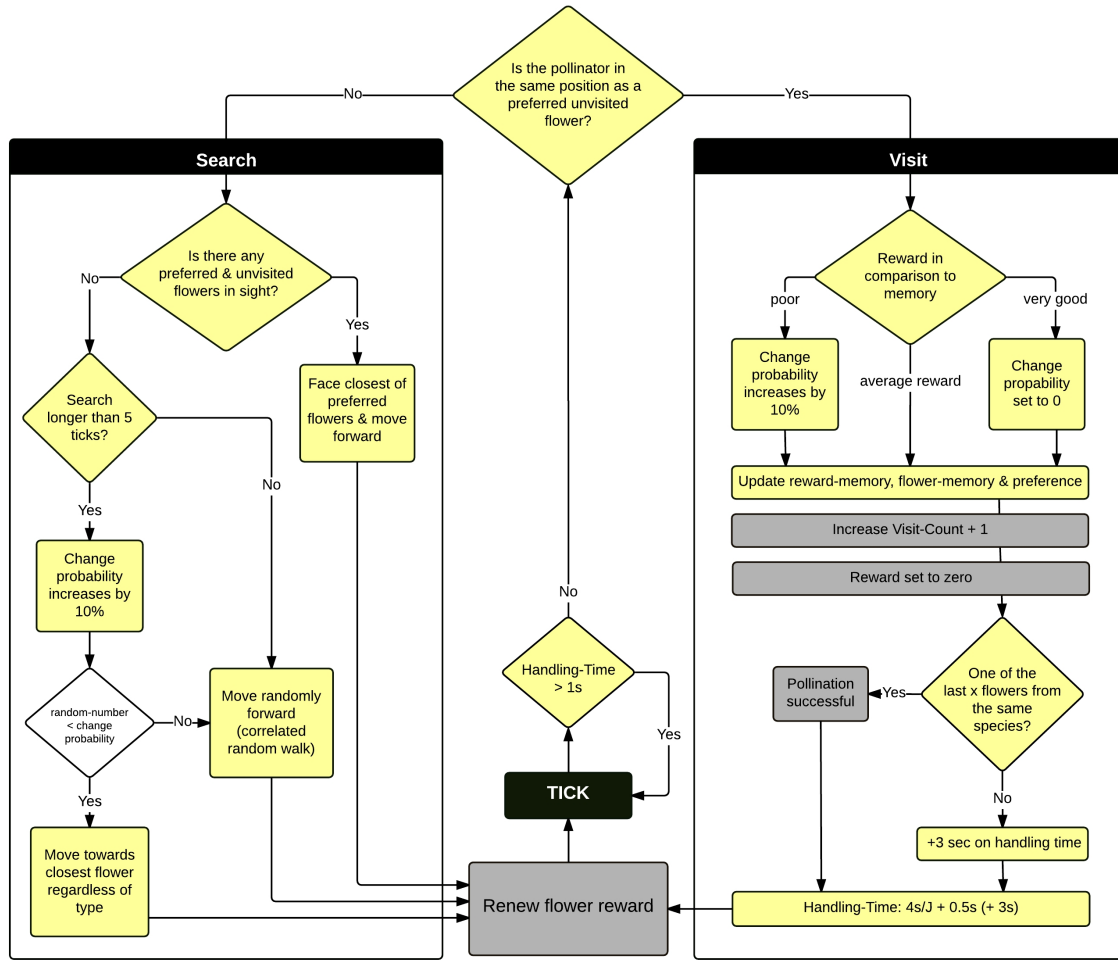
Figure 2: Flowchart describing the behavior rules for the bee-agents within the agent-based model. Every bee-agent can either search for a preferred flower or visit one. While searching, a bee-agent can remember the location of the last four visited flowers to avoid double-encountering. If there is no flower in sight after 5 seconds of correlated random walk (CRW), the probability that it will encounter the next available flower despite its type increases by 10% per additional time step. When a bee-agent visits a flower it takes all reward within a reward-dependent handling time and compares the amount with its memory. If the reward is low, the agent is more likely to visit the other flower type next time. The maximum of visits within a successful pollination is possible is determined by the pollen carryover rate.

3.2 Results

Global visitation

The sum of visits are not evenly distributed for all frequency stages (Fig. ??). A strong cover-dependent pattern is visible for small cluster values. The visits have a u-shaped relationship for 5% cover and a fourth-degree polynomial function for higher cover values. The visitation drops to a minimum at 90:10 ratio and peaks again for balanced frequencies. Cluster reduce the frequency dependence.

Note that the absolute visitation numbers vary additional to the shape for cover and cluster values. Both parameters have a frequency independent influence on the visitation rate (supplementary material, fig. S4). Floral cover shows a Hollings type II functional response saturated at 30% and the visits for degree of clustering have a hump-shaped relationship with a peak at an intermediate agglomeration level of 5-10 flowers per cluster.

Table 1: Parameter values used for the main and sensitivity analysis. Only general parameters were changed in the main analysis, whereas the sensitivity analysis also directly influences the behavior of the bee-agents. Within the main analysis, each combination was run 20 times for 1000 ticks (total of 110400 simulation runs)

Parameter	Description	Values
MAIN ANALYSIS		
Frequency	Proportion of species A on all flowers	0-100% (5%-steps)
Flower cover	Proportion of patches being flowers	5, 10, 20, 50 %
Degree of clustering	Average number of flowers per cluster	1, 2, 5, 10, 20, 50, 75, 100
Pollen-carryover rate	Number of visits within a successful pollination is possible	1, 2, 4, 6, 8, 16
SENSITIVITY ANALYSIS		
Reward function	Increase of reward per flower and second	0, 0.00004, 0.001, 0.1 J/sec
Vision distance	Max. range of patches within a bee-agent can detect flowers	1, 6, 20, 50 patches
Search time	Number of seconds a bee-agent searches before probability of switching flowers increases	1, 5, 20, 50 sec
Pollinator density	Number of bee-agents on the meadow	5, 10, 20, 50 bees

Per-flower visitation rate

The per-flower visitation shows a similar cubic function as the data collected in the Jena Experiment (Fig. ??A,B). Within the first 20% there is a steep increase in visits per flower. Afterwards, additional gain of visits is for all cover values above 5% not proportional with the increase of flowers due to higher frequency, the per-flower visitation drops with a minimum around 80%. Towards 100%, when the species gets exclusive, the per-flower visitation rises again. Cover and cluster both influence the frequency dependence. The higher the cover, the lower the per-flower visitation and the bigger the cluster the less visible is the frequency dependence. Simulations with more than 10 flowers per cluster show a high variance for frequencies below 10% and very low to no frequency dependence afterwards (Fig. ??C,D).

The same data is plotted as proportion of visits to species A to take the variance in the sum of visits into account (Fig. ??E-H; see previous section "Global visitation"). It shows a clear negative frequency dependence favoring the rare specie. Below 50%,species A gets more visits than would be proportional, above 50% the curve is mirrored because both species are identical in the simulation and the common species gets unproportional few visits. The higher the cover, the stronger is the frequency dependence. For higher cluster values, all data points approach a frequency independent relationship (Fig. ??H).

Pollination ratio

The pollen-carryover rate is defined as maximum number of visits within a successful pollination can take place. In the model, I tested values from 1 (strong heterospecific pollen interference) to 16 (weak heterospecific pollen interference). Figure ?? gives the proportion of all visits where a successful pollination took place. The first 20% frequency are crucial for all parameter-value combination. A very steep increase up to 80% successful pollinated flowers is followed by a moderate linear increase up to 100% for exclusive existence. The pollen-carryover rate only makes a difference for small cover and cluster values (Fig. ??a). The higher the cover and the bigger the cluster, the better is also the proportion of successful pollination, even for small frequencies, independent of the pollen-carryover rate(Fig. ??c,f,g-i).

Sensitivity analysis

Aim of the sensitivity analysis is the understanding of the underlying behavior parameters on the outcome of the model. Therefore, pollinator density, reward regrowth, search time and vision were tested for a (unnaturally) broad range of values and analyzed as proportional data to check for difference to the empirically founded default values. Vision, search time and the number of bees on the meadow influence the sum of visits

(Fig. S5). A higher vision leads to more visits in a saturated curve, the search limit reduces the number of visits and more bees lead again to more visits per time unit. The reward function has only for a very high regrowth rate an small negative influence on the total number of visits.

Reward regrowth

Only a considerably high regrowth rate (0.1J/sec, yellow line in fig. S6) has a reversing effect on the frequency dependence: Rare species get unproportionally few visits whereas common species benefit from a positive frequency dependence. The influence is less severe with increasing cluster size.

Pollinator vision distance

Every bee-agent can detect flowers in a 180° cone-shaped array of patches to their front. The number of patches in that array is determined by the vision distance. A high vision increases the sigmoid frequency dependence even in a heavily clustered model environment (Fig. S7). If the bee-agents are only able to see the direct neighbor, the frequency dependence is reversed to favor the common species for low cluster values.

Search time limit

If a bee-agent searches longer than a given search time limit unsuccessfully for a unvisited and preferred flower, the probability to switch preferences will increase by 10% with every additional step. The search limit was altered from 1 to 50 seconds in the sensitivity analysis. The results are similar to the effect of vision as they also change the probability to switch preferences. Higher search time limits lead to stronger negative frequency dependence benefiting the rare species. A search limit of 1 second reduces the dependency (Fig. S8).

Pollinator density

Besides the expected increase of absolute visits, a change of pollinator density has no effect on the outcome of the model at any cover or cluster values (Fig. S9).

4 Discussion

Frequency dependence can have far reaching consequences for the development and maintaining of biodiversity. Aim of this thesis is to study the existence of frequency dependence in a natural plant community for the first time, explore the kind of relationship and understand the underlying rules and drivers for frequency dependence with the help of an agent-based model. The results of the natural condition data are consistent with the simulation data: We were able to find a distinct frequency dependence within the per-flower visitation rate (cf. fig. ?? and fig. ??A). The relationship is defined by a a steep increase of visits within the first 20% occurrence followed by a unproportional low gain of visits for every additional flower until the flower becomes exclusive and the per-flower visitation rate increases again. Additional simulations confirms the negative frequency dependence as outcome of the empirical based default values.

Explaining negative frequency dependence

The field data suggests a negative FD for at least four different rewarding flower species confirmed by the results from the foraging simulation whereas previous research found positive FD for lab experiments and inconsistence in the few field experiments with color morphs (review by Smithson 2001). Where does the discrepancy of lab and field data comes from? The sensitivity analysis of the ABM can give an explanation: If the reward function is increased to a refill within 10 ticks, the relationship reversed to a positive frequency dependence (Fig. S6) and the rare species gets unproportionally few visits. The curve is highly consistent with findings of Smithson and Macnair (1997) and Smithson and Macnair (1996) in their lab experiments. On the bee-board, artificial flowers were refilled after each foraging bout. Therefore, every bumble bee got a fresh set of equally rewarding flowers to forage on which is comparable to a high regrowth function in the ABM. It is known that pollinators change constancy if they experience bad reward (Chittka et al., 1997) and if the reward is always high, bee-agents have less incentive to go on exploratory visits to the rare species as the abundant type is easy to find and sufficient rewarding. Hence it can be assumed that negative frequency dependent selection does not exclusively apply for non-rewarding species but also for flowering communities with varying or intermediate to low reward. Positive frequency dependence in pollination might be only possible for highly rewarding or artificial systems as is was If negative frequency dependence is in fact found for a variety of rewarding flowers, I agree with Eckhart et al. (2006) that frequency dependence might be more important in the development and conservation of diversity then previously recognized. More research, especially on natural field conditions, is needed to confirm this hypothesis.

Cover and Cluster as important drivers

The model reveals two drivers for frequency dependence: The higher the floral cover, the stronger the frequency dependence and the bigger the clusters, the lower the frequency dependence (Fig. ??E-H). Floral density is known to influence visitation rates, usually positive and with a saturating function (e.g.Essenberg 2012, Bernhardt et al. 2008, Kunin 1997). Those findings are consistent with the functional response found for different cover values (Supplementary material, fig. S4a). If the cover is increasing, the absolute number of flowers rises also for the rare species. That makes it more likely for a bee-agent to find a flower before changing preference towards the common species even if foraging on the later would be more efficient. High cover causes the same effect as expanded vision distance or maximum search limit (cf. fig. S7 and fig. S8): The main reason of abandoning flower constancy becomes multiple visit of flowers with low reward. Furthermore, every visit to a rare species weights high in the per-flower visitation rate because the sum of visits is divided through the number of flowers. Even few "exploratory" visits can have great impact on the proportion.

The model shows that spatial agglomeration of flowers can lead to a more efficient foraging (more visits per time unit), less FD and a higher quality of visits due to compatible pollen deposits. If flowers are evenly distributed, many short search and flight times apply. A intermediate cluster level is easy to exploit by a pollinator whereas the flight and search times can be very long in between few big cluster, especially for low floral densities (Supplementary material, fig. S4b). It was already suggested by Epperson and Clegg (1987) that spatial agglomeration of flowers decreases frequency dependence. In the model, a similar effect as with low

cover takes place: If flowers are agglomerated at few places, they are more difficult to find for a bee-agent with limited vision. They will change preferences due to long search times and forage efficiently on the next best cluster.

Requirements for successful pollination

Optimal visitation rate is gained at low frequency with high cover and low cluster values. Those visits might not be the best quality if the pollination per visit ratio is comparatively low (Fig. ??a,d). The ratio can be seen as index for flower constancy: If the majority of visits lead even for small pollen-carryover to a successful pollination the bee-agents behave strongly after the theory of constancy (Montgomery, 2009). If the cover is high enough, bee-agents will keep their constancy also for rare species because they are abundant enough. If the agglomeration of flowers is high, bee-agents exploit this cluster before leaving for the next. Every visit within a cluster of flowers of the same species is counted as successful pollination and can lead to a high visit quality even if the cover is low (cf.Jakobsson et al. 2009)

Therefore it would be optimal for rare flowers to stand in clusters of flowers if the cover is low to get sufficient pollination. If the cover is high the spatial distribution plays a minor role for the visit quality.

Frequency dependence exists also on sum of visits to the flower community

Additionally to individual frequency dependence, I analyzed the impact of species partitioning on frequency dependent visitation the system as whole. Unfortunately, this part of frequency dependence lacks completely in previous research.

If the cover is very low, most visits can be gained if one species is exclusive. Co-flowering will lead to longer search times and less overall visits (u-shape for 5% cover in fig. ??a). For higher cover, the frequency dependence shows a fourth-degree polynomial relationship. If one species is rare at 5-20%, some bee-agents will still have at least exploratory visits to the rare species and spend inefficient time searching, the total visitation number drops to a minimum. If species are even distributed the pollinators forage on both species in equal amounts. This is the most efficient status for the overall ecosystem, especially for high covers or spatial agglomeration.

A higher spatial agglomeration weakens the frequency effect but will also reduce the total visits. If flowers are evenly and random distributed, the bee-agent has many small search times intermittent by collecting reward on a single flower and continue foraging. Rare flowers can be found comparatively easy if they are spread over the whole meadow and flower constancy will be kept even if it is highly inefficient. If the clusters of flowers are bigger, bee-agents will not find rare flowers that easily because they might occur only in a single cluster on the meadow. The bee-agent will switch to the common flower, the minimum at very uneven distribution disappears and the relationship becomes slightly hump-shaped (see Fig. ??b,c).

For both the pollinators and the co-flowering plants the ABM suggests to have even frequency for high cover and very uneven for low cover. An intermediate degree of clustering also improves the absolute number of visits, species partitioning gets less important. These findings should be verified by manipulated field experiments. Natural conditions data like sampled in the Jena Experiment are not suitable for this purpose because every plot contains more than two co-flowering species with unequal attractiveness.

Limitations of the study design and future research suggestions

Even though modeling can be an excellent tool to understand and interpret ecological data, some questions evolve comparing the data collected in the Jena Experiment and the foraging model. Floral cover is an important factor in the outcome of the model. It influences not only the absolute number of visits but also the intensity of frequency dependence. But it was removed in the model selection as it was no factor of explanatory power to the per-flower visitation data. Reason could lie in the sampling design. Data was only observed from plots with an intermediate cover, no extremes were taken into account. In total, there were only five values for cover in the final analysis. Also all cover values are estimations, no exact measurements. Another drawback are the lack of data for cluster values and pollination success. The experimental design and time restraints made it impossible to take more predictors into account. The data collected in Jena shows drastic

differences in attractiveness of the focal species. Also, frequency dependence was found to be subject to each species. Therefore I strongly suggest research on a variety on species, both rewarding and unrewarding in natural occurring flower communities and manipulated simple two-species systems. Necessary to validate further results of the ABM would be a supplementary study with manipulated frequency, cover and cluster values of only two co-flowering species. Either under natural conditions where manipulation is possible (eg. Eckhart et al. 2006; Essenberg 2012) or with potted plants (Epperson and Clegg, 1987).

5   Conclusions

1. "in conclusion, our study shows (what you think is the main message)"
    2."Important for our understanding of ..."
    3."Based on our findings, we recommend ..."
    4."Further research is necessary to finally establish ..."
    5. Suggest practical applications of your results? - More knowledge about pollination always good: Big environmental factor (diodiversity, function of ecosystems, economically) - Not direct practical applicable - maybe: how to integrate other flowering plants to enhance pollination in crop production?

Here, the combination of methods is exceptionally helpful to understand underlying drivers. The interpretation of ecological results is often based on guesses. With a combination of methods,an methodically exploration of reasons is possible.

more connection of modeling, field and lab work. Most research is only done in one of those three approaches. Crossvalidation is missing. It can be gained a lot by getting the field-loving outdoor-ecologists and the computer-statistic-geeks working more together. NetLogo is learnable in a reasonable short time, even for non-statistitians.

Extent model:

- integrate metalevel in model/ multiple plots in one world

- more species

- similarity gradient

General outcome: cover increases frequency dependence because also the rare species is more abundant and clustering decreases frequency dependence because if flowers are clustered, they are again more difficult to find. A rare species gets the most visits in a high cover and low cluster environment.

References

Barton, K. (2014). *MuMIn: Multi-Model Inference*. R package version 1.12.1.

Bartumeus, F., da Luz, M. G. E., Viswanathan, G., and Catalan, J. (2005). Animal search strategies: a quantitative random-walk analysis. *Ecology*, 86(11):3078–3087.

Benadi, G., Blüthgen, N., Hovestadt, T., and Poethke, H.-J. (2012). Population dynamics of plant and pollinator communities: stability reconsidered. *The American Naturalist*, 179(2):157–168.

Bernhardt, C. E., Mitchell, R. J., and Michaels, H. J. (2008). Effects of population size and density on pollinator visitation, pollinator behavior, and pollen tube abundance in lupinus perennis. *International Journal of Plant Sciences*, 169(7):944–953.

Bever, J. (1999). Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. *Ecology Letters*, 2(1):52–61.

Bobisud, L. E. and Neuhaus, R. J. (1975). Pollinator constancy and survival of rare species. *Oecologia*, 21(3):263–272.

Bukovac, Z., Dorin, A., and Dyer, A. (2013). A-bees see: a simulation to assess social bee visual attention during complex search tasks. *Advances in Artificial Life, ECAL*, 12:276–283.

Campbell, D. R. (1986). Predicting plant reproductive success from models of competition for pollination. *Oikos*, pages 257–266.

Chittka, L., Gumbert, A., and Kunze, J. (1997). Foraging dynamics of bumble bees: correlates of movements within and between plant species. *Behavioral Ecology*, 8(3):239–249.

Chittka, L., Thomson, J. D., and Waser, N. M. (1999). Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften*, 86(8):361–377.

Codling, E. A., Plank, M. J., and Benhamou, S. (2008). Random walk models in biology. *Journal of the Royal Society Interface*, 5(25):813–834.

DeAngelis, D. L. and Mooij, W. M. (2005). Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution, and Systematics*, pages 147–168.

Dornhaus, A., Klügl, F., Oechslein, C., Puppe, F., and Chittka, L. (2006). Benefits of recruitment in honey bees: effects of ecology and colony size in an individual-based model. *Behavioral Ecology*, 17(3):336–344.

Dyer, A., Dorin, A., Reinhardt, V., Garcia, J., and Rosa, M. (2014). Bee reverse-learning behavior and intra-colony differences: Simulations based on behavioral experiments reveal benefits of diversity. *Ecological Modelling*, 277:119–131.

Dyer, A. G., Spaethe, J., and Prack, S. (2008). Comparative psychophysics of bumblebee and honeybee colour discrimination and object detection. *Journal of Comparative Physiology A*, 194(7):617–627.

Eckhart, V., Rushing, N., Hart, G., and Hansen, J. (2006). Frequency-dependent pollinator foraging in polymorphic clarkia xantiana ssp. xantiana populations: implications for flower colour evolution and pollinator interactions. *Oikos*, 112(2):412–421.

Elliott, S. E. and Irwin, R. E. (2009). Effects of flowering plant density on pollinator visitation, pollen receipt, and seed production in delphinium barbeyi (ranunculaceae). *American Journal of Botany*, 96(5):912–919.

Epperson, B. K. and Clegg, M. T. (1987). Frequency-dependent variation for outcrossing rate among flower-color morphs of ipomoea purpurea. *Evolution*, pages 1302–1311.

Essenberg, C. J. (2012). Explaining variation in the effect of floral density on pollinator visitation. *The American Naturalist*, 180(2):153–166.

Faruq, S., McOwan, P. W., and Chittka, L. (2013). The biological significance of color constancy: An agent-based model with bees foraging from flowers under varied illumination. *Journal of vision*, 13(10):10.

Gigord, L. D., Macnair, M. R., and Smithson, A. (2001). Negative frequency-dependent selection maintains a dramatic flower color polymorphism in the rewardless orchid dactylorhiza sambucina (l.) soo. *Proceedings of the National Academy of Sciences*, 98(11):6253–6255.

Goulson, D. (1994). A model to predict the influence of insect flower constancy on interspecific competition between insect pollinated plants. *Journal of Theoretical Biology*, 168(3):309–314.

Goulson, D. (1999). Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. *Perspectives in Plant Ecology, Evolution and Systematics*, 2(2):185–209.

Goulson, D. (2000). Why do pollinators visit proportionally fewer flowers in large patches? *Oikos*, 91(3):485–492.

Goulson, D., Ollerton, J., and Sluman, C. (1997). Foraging strategies in the small skipper butterfly,¡ i¿ thymelicus flavus¡/i¿: when to switch? *Animal Behaviour*, 53(5):1009–1016.

Goulson, D. and Wright, N. P. (1998). Flower constancy in the hoverflies episyrphus balteatus (degeer) and syrphus ribesii (l.)(syrphidae). *Behavioral Ecology*, 9(3):213–219.

Hanoteaux, S., Tielbörger, K., and Seifan, M. (2013). Effects of spatial patterns on the pollination success of a less attractive species. *Oikos*, 122(6):867–880.

HILL, P. S., WELLS, P. H., and WELLS, H. (1997). Spontaneous flower constancy and learning in honey bees as a function of colour. *Animal Behaviour*, 54(3):615–627.

Jakobsson, A., Lázaro, A., and Totland, Ø. (2009). Relationships between the floral neighborhood and individual pollen limitation in two self-incompatible herbs. *Oecologia*, 160(4):707–719.

Jones, K. N. (1996). Pollinator behavior and postpollination reproductive success in alternative floral phenotypes of clarkia gracilis (onagraceae). *International Journal of Plant Sciences*, pages 733–738.

Keasar, T., Shmida, A., and Motro, U. (1996). Innate movement rules in foraging bees: flight distances are affected by recent rewards and are correlated with choice of flower type. *Behavioral Ecology and Sociobiology*, 39(6):381–388.

Kluge, G., Müller-Westermeier, G., and Wetterdienst, D. (2000). *Das Klima ausgewählter Orte der Bundesrepublik Deutschland: Jena*. Selbstverlag des Deutschen Wetterdienstes.

Kunin, W. and Iwasa, Y. (1996). Pollinator foraging strategies in mixed floral arrays: density effects and floral constancy. *Theoretical population biology*, 49(2):232–263.

Kunin, W. E. (1991). *Few and far between: plant population density and its effects on insect-plant interactions*. PhD thesis, University of Washington.

Kunin, W. E. (1993). Sex and the single mustard: population density and pollinator behavior effects on seed-set. *Ecology*, pages 2145–2160.

Kunin, W. E. (1997). Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of brassica kaber. *Journal of Ecology*, pages 225–234.

Molofsky, J. and Bever, J. D. (2002). A novel theory to explain species diversity in landscapes: positive frequency dependence and habitat suitability. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269(1508):2389–2393.

Montgomery, B. R. (2009). Do pollen carryover and pollinator constancy mitigate effects of competition for pollination? *Oikos*, 118(7):1084–1092.

Morris, W. F., Vázquez, D. P., and Chacoff, N. P. (2010). Benefit and cost curves for typical pollination mutualisms. *Ecology*, 91(5):1276–1285.

Ne'eman, G. and Kevan, P. G. (2001). The effect of shape parameters on maximal detection distance of model targets by honeybee workers. *Journal of Comparative Physiology A*, 187(8):653–660.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team (2014). *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-117.

Pyke, G. and Cartar, R. (1992). The flight directionality of bumblebees: do they remember where they came from? *Oikos*, pages 321–327.

R Core Team (2014). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rands, S. A. and Whitney, H. M. (2010). Effects of pollinator density-dependent preferences on field margin visitations in the midst of agricultural monocultures: A modelling approach. *Ecological Modelling*, 221(9):1310–1316.

Roscher, C., Schumacher, J., Baade, J., Wilcke, W., Gleixner, G., Weisser, W. W., Schmid, B., and Schulze, E.-D. (2004). The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology*, 5(2):107–121.

Roubik, D. W. (1992). *Ecology and natural history of tropical bees*. Cambridge University Press.

Smithson, A. (2001). Pollinator preference, frequency dependence, and floral evolution. *Cognitive ecology of pollination: Animal behaviour and evolution, Cambridge Univ. Press, Cambridge*, pages 237–257.

Smithson, A. and Macnair, M. (1996). Frequency-dependent selection by pollinators: mechanisms and consequences with regard to behaviour of bumblebees bombus terrestris (l.)(hymenoptera: Apidae). *Journal of Evolutionary Biology*, 9(5):571–588.

Smithson, A. and Macnair, M. R. (1997). Density-dependent and frequency-dependent selection by bumblebees bombus terrestris (l.)(hymenoptera: Apidae). *Biological Journal of the Linnean Society*, 60(3):401–417.

Smithson, A. and MacNair, M. R. (1997). Negative frequency-dependent selection by pollinators on artificial flowers without rewards. *Evolution*, pages 715–723.

Stout, J. C., Allen, J. A., and Goulson, D. (1998). The influence of relative plant density and floral morphological complexity on the behaviour of bumblebees. *Oecologia*, 117(4):543–550.

Thiele, J. C., Kurth, W., and Grimm, V. (2012). Rnetlogo: An r package for running and exploring individual-based models implemented in netlogo. *Methods in Ecology and Evolution*, 3:480–483.

Thomson, J. D. (1981). Field measures of flower constancy in bumblebees. *American Midland Naturalist*, pages 377–380.

Viswanathan, G., Raposo, E., and Da Luz, M. (2008). Lévy flights and superdiffusion in the context of biological encounters and random searches. *Physics of Life Reviews*, 5(3):133–150.

Waddington, K. D. (1980). Flight patterns of foraging bees relative to density of artificial flowers and distribution of nectar. *Oecologia*, 44(2):199–204.

Waser, N. M. (1986). Flower constancy: definition, cause, and measurement. *American Naturalist*, pages 593–603.

Wertlen, A. M., Niggebrügge, C., Vorobyev, M., and de Ibarra, N. H. (2008). Detection of patches of coloured discs by bees. *Journal of Experimental Biology*, 211(13):2101–2104.

Wilensky, U. (1999). Netlogo. *Center for Connected Learning and Computer-Based Modeling, Northwestern University. Evanston, IL.*

Zuur, A., Ieno, E. N., and Smith, G. M. (2007). *Analysing ecological data.* Springer Science & Business Media.

Supplementary Material

Table S1: List of the focal species observed in the natural condition experiment within the area of the Jena Experiment. Species had to flower in at least five plots with different frequency values.

Short	Name	German Name	Order	Family	Color
Ger	*Geranium pratense*	Wiesen-Storchschnabel	Geraniales	Geraniaceae	Purple
Lat	*Lathyrus pratensis*	Wiesen-Platterbse	Fabales	Fabaceae	Yellow
Lot	*Lathyrus pratensis*	Gewöhnliche Hornklee	Fabales	Fabaceae	Yellow
Ono	*Onobrychis viciifolia*	Saat-Esparsette	Fabales	Fabaceae	pink+white
TP	*Trifolium pratense*	Wiesen-Klee	Fabales	Fabaceae	Purple
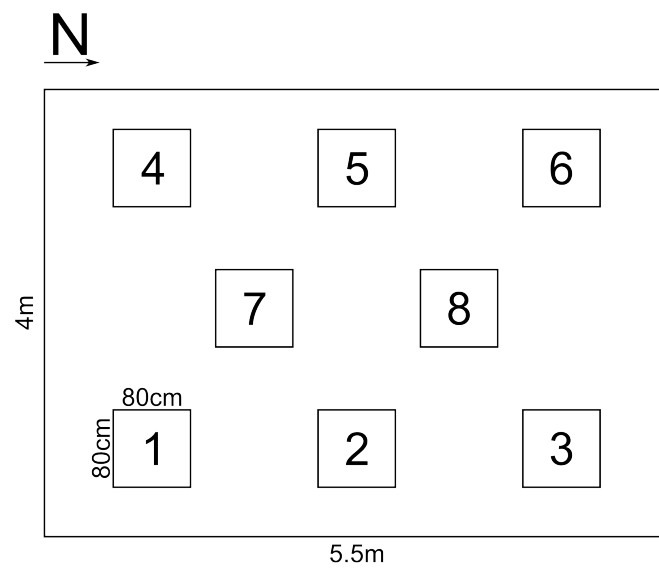
Figure S1: The distribution of subplots within the old invasion plots.
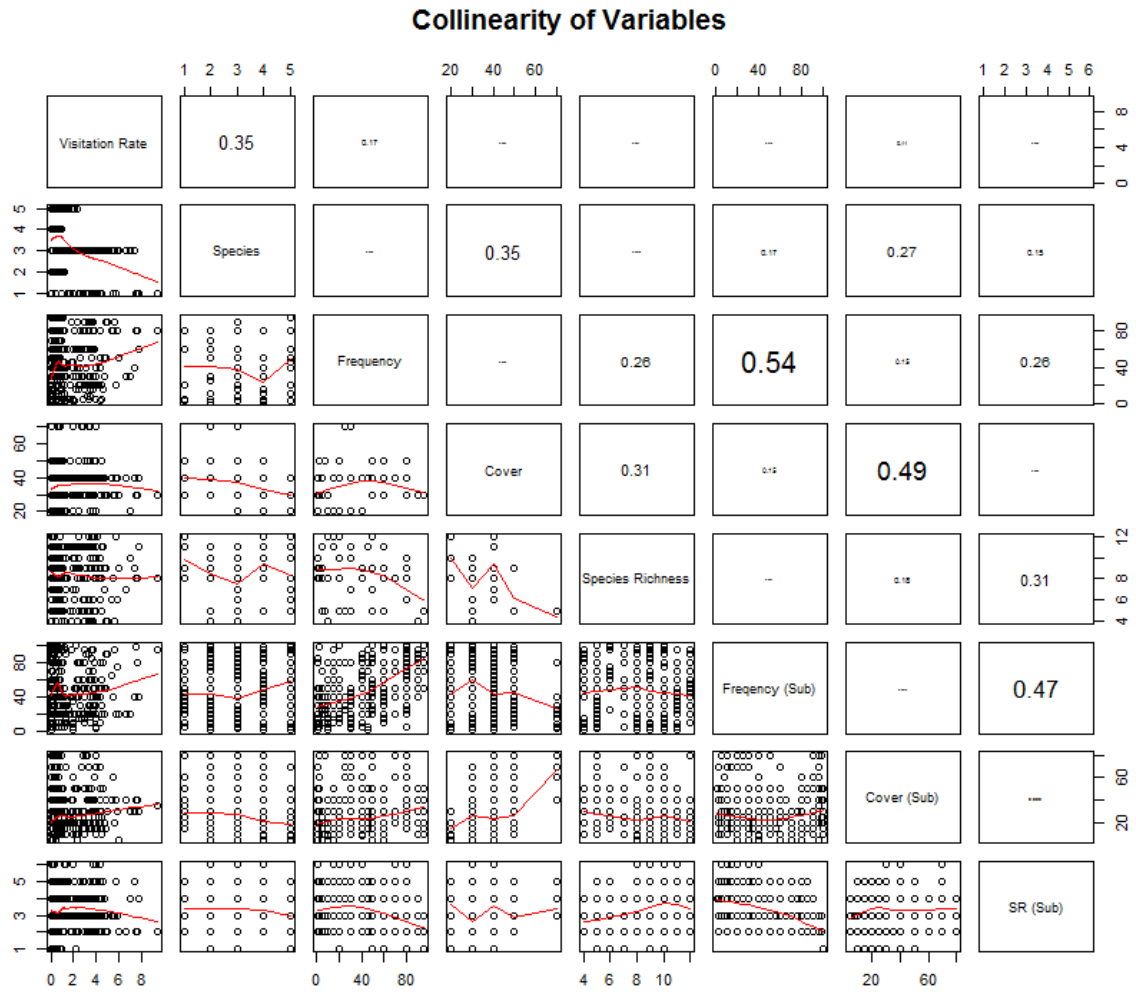
Collinearity of Variables

Figure S2: Pairwise correlation of Visitation rate (response variable), species, frequency, floral cover and species richness on plot and subplot-level. The upper panels contain Pearson correlation coefficients with its size proportional to its value. Parameters correlate on the plot and subplot level but show no strong correlation not among each other.

Table S2: Variance inflation factors (VIF) for the full set of variables. Values are calculated by the "corvif"-function from R-package AED. All values are well below three indicating no collinearity (see Zuur et al. (2007)).

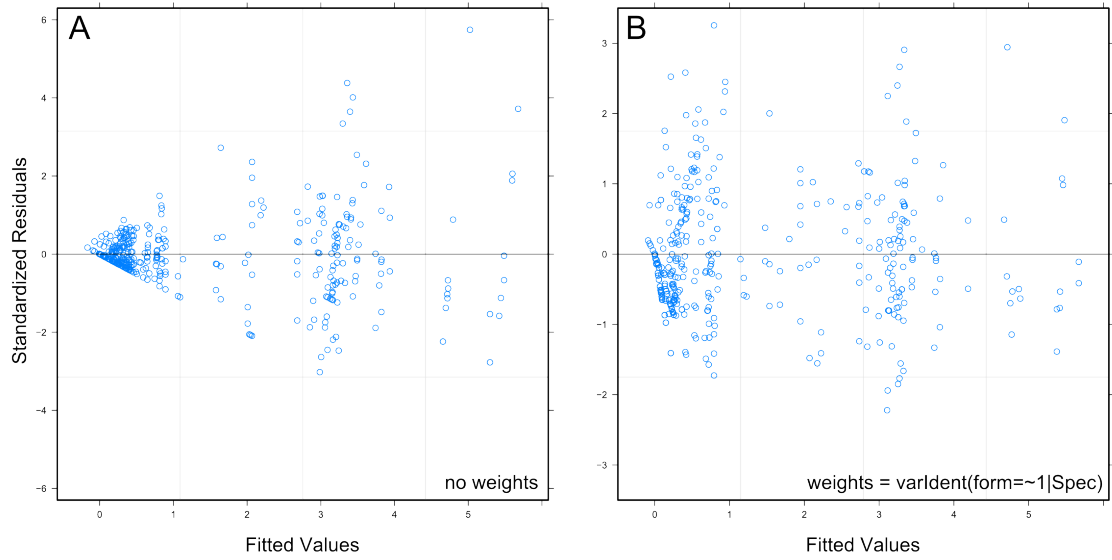| Variable	GVIF
Visitation Rate	1.19
Species	1.36
Frequency	1.61
Floral Cover	1.57
Species Richness	1.36
Frequency (Subplot)	1.83
Floral Cover (Subplot)	1.38
Species Richness (Subplot)	1.48

Figure S3: Standardized residuals plotted against fitted values for the final mixed effect model with and without applied weighting. A) Without weighting, the residuals show strong pattern of heteroscedasticy. B) The weighting allows different variance per species. The final model is significantly better with weighting (L=393.32, df= 4, $P < 0.0001$)

Table S3: Extended output from the linear mixed effect model. Floral cover and species richness were removed in the model selection

| Expanatory Variables	Estimate	$\pm$ SE	P
Intercept (Ger)	1.41	0.49	0.0048
Lat	-1.58	0.58	0.0069
Lot	-1.38	0.51	0.0075
Ono	-1.31	1.06	0.2182
TP	-1.39	0.5	0.0060
Frequency	0.11	0.05	0.0147
$Frequency^2$	-0.002	< 0.01	0.0699
$Frequency^3$	< 0.01	< 0.01	0.1174
Frequency x Lat	-0.09	0.05	0.0925
Frequency x Lot	-0.09	0.05	0.0687
Frequency x Ono	0.32	0.14	0.0183
Frequency x TP	-0.1	0.05	0.0425
$Frequency^2$ x Lat	< 0.01	< 0.01	0.1013
$Frequency^2$ x Lot	< 0.01	< 0.01	0.2053
$Frequency^2$ x Ono	-0.01	< 0.01	0.0113
$Frequency^2$ x TP	< 0.01	< 0.01	0.1479
$Frequency^3$ x Lat	> -0.01	< 0.01	0.0966
$Frequency^3$ x Lot	> -0.01	< 0.01	0.2996
$Frequency^3$ x Ono	< 0.01	< 0.01	0.0086
$Frequency^3$ x TP	> -0.01	< 0.01	0.2283
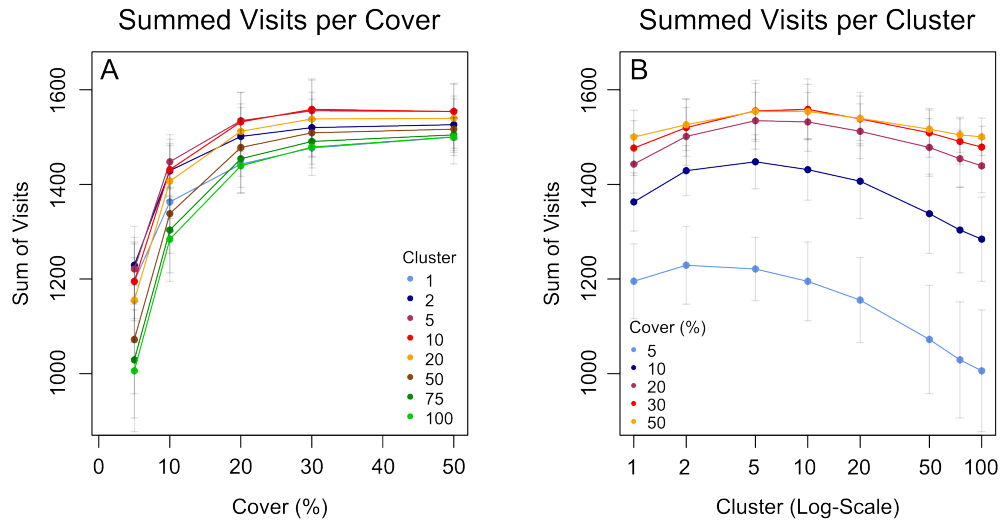
Figure S4: Frequency independent influence of floral cover and degree of flower agglomeration on the summed visits within one simulation run. Cover strongly influences the number of visits as it reduces the flight and search time. Plot A shows a saturated relationship for all cluster values. This matches the Hollings type II functional response. B) The degree of clustering also determines the sum of visits in a hump-shaped function. The maximum (depending on the cover) lays between 5 and 10 flowers per cluster. A small agglomeration of flowers reduces search times but keeps the next patch within short distance. The bigger the cluster, the more difficult to find the next one.

Table S4: The full set of parameters and default values used in the model.

| Parameter	Description	NetLogo-Type	Type	Value	Reference
SETUP PARAMETERS:					
area	"world" in NetLogo, number of grid-cells		integer	100x100	
patch-size	Size one grid-cell in NetLogo. Can be either a flower or grass		float	0.1m²	
tick	One time-unit in NetLogo		integer	1s	
flower-cover	Proportion of grid cells containing a flower	global	integer	5, 10, 20, 30, 50	
frequency	Proportion of flowers which are species A feq(B) = 100 - freq(A)	global	integer	0-100%	
cluster-number	Average number of flowers per cluster	global	integer	1, 2, 5, 10, 20, 50, 75, 100	
number-bees	Initial number of pollinators in the model	global	integer	10	0.0004 - 1 bee/m² (Essenberg, 2012)
BEHAVIOURAL PARAMETERS:					
search-speed	Distance a pollinator can move per tick	bees-own	integer	0.1m /sec	(Kunin, 1991) in (Kunin and Iwasa, 1996) 0.09-0.17 (Essenberg, 2012)
stdev-angle	Standard deviation for the normal distribution used in the CRW	global	integer	30	Waddington 1980
flightsteps-until-change	seconds of unsuccessful search before the constancy changes	bees-own	integer	5s (= 5 ticks)	Chittka et al. 1997
length-memory	How many flowers can a bee remember to avoid double-visiting.	bees-own	integer	4	Goulson 2000, see Goulson 1999 for review
view	Value for the radius of grid-cells a pollinator can see (cone-view of 180°)	bees-own	integer	0.7m (= 6 grid-cells)	(Dyer et al., 2008; Wertlen et al., 2008) Ne'eman and Kevan 2001
array	Array of all suitable flowers (referred, non-visited) flowers in sight of the pollinator	bees-own	Array		
reward-function	How fast the reward is renew per second	flowers-own	float	0.00004 J/s	
handling-time	The time a pollinator needs for exploiting the floral reward	bees-own	integer	reward * 4s + 0.5s (+ 3s)	Roubik 1992 in Kunin and Iwasa 1996
reward	Reward in Joule the flower has to offer. Exploited with each visit, renewed over time	flowers-own	float	reward(max) = 1J	Kunin 1991 in Kunin and Iwasa 1996
pollen carry-over rate	The max. number of visits within a successful pollination is possible	flowers-own	integer	1, 2, 4, 6, 8, 16	
flower-memory	A list of flower-locations	bees-own	string	4	Benadi et al. 2012
reward-memory	A list of the last gained rewards	bees-own	string	4	see Goulson 1999 for review)
change-prob	Probability to change the preferred flower type. Increases with low reward and long search times	bees-own	float		
choice	Current flower choice for the pollinator (for constancy)	bees-own	boolean		
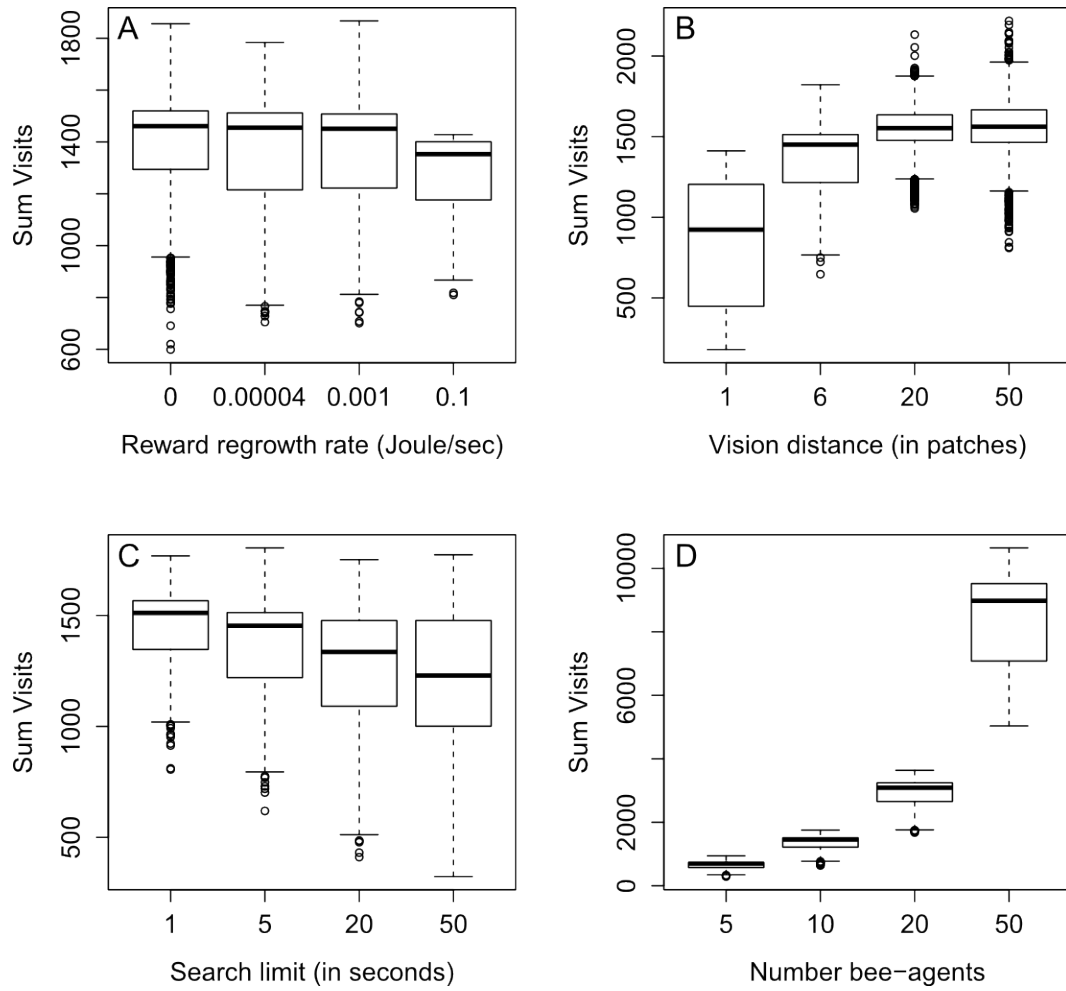
Figure S5: The influence of reward regrowth, vision, search limit and number of bee-agents on the total visits within a 1000 tick simulation run. A) Only an unnatural high reward regrowth has a small negative influence on the visits. B) Bee-agents with a far field of view can detect flowers faster, move in a direct way towards them and be therefore more efficient. However, the curve is saturated at a view of 20 patches. C) An increase in search time limit decreases the sum of visits and spread the variance. Bees-agents will keep searching for rare flowers instead of switching to the common species. D) As assumed, more bees lead to more visits.
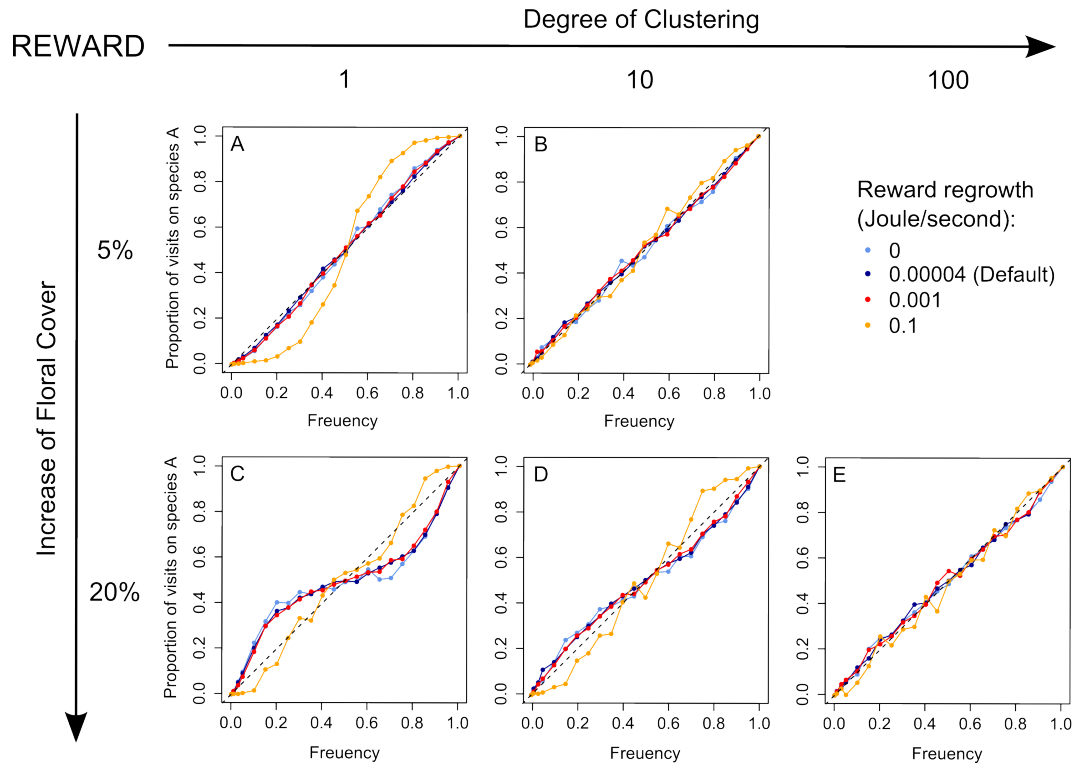
Figure S6: Outcome of the model if the reward regrowth function is changed to 0, 0.004, 0.001 and 0.1 Joules per second. Only the unnatural high reward function (complete regrowth after 10 seconds) has an influence on the frequency dependence: the bee-agents have no more reason to change preference due to bad reward gained. This favors the more common species as shown in the opposite curving for no-cluster environments. A lower regrowth rate has no effect.
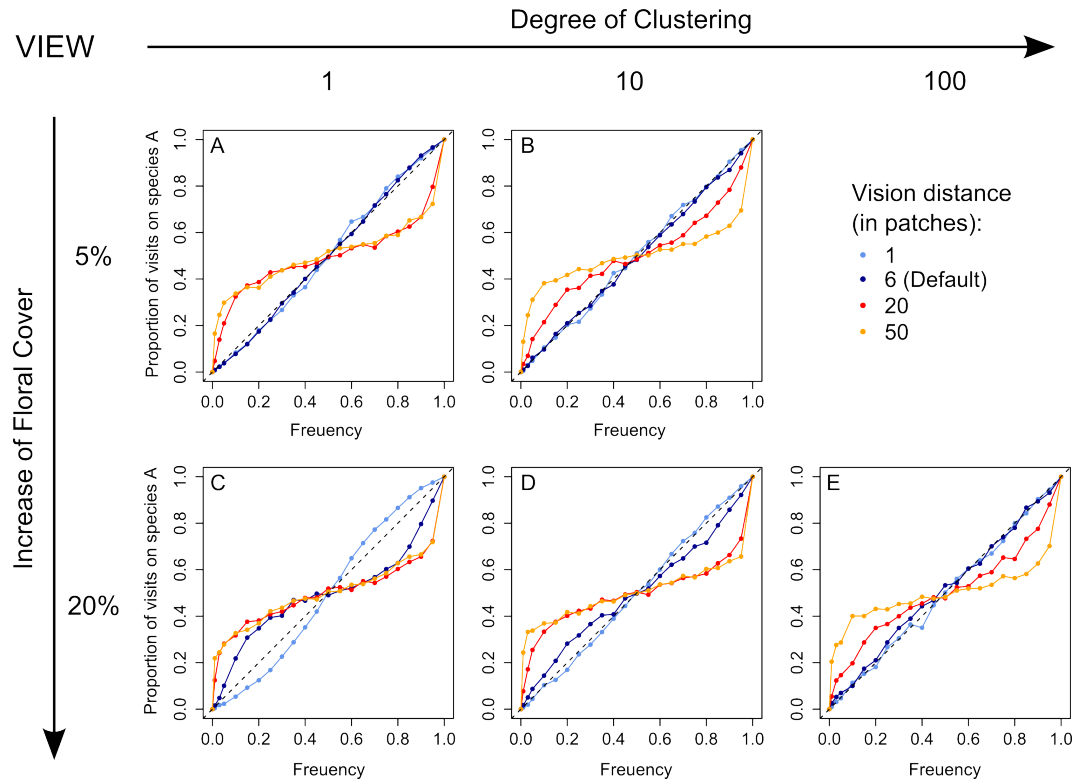
Figure S7: Effect of increased or reduced vision for the bee-agent. The vision influences the behavior of the bee-agent. If sees far, it can move on direct way towards the next preferred flower and saves searching time. But it also more often fly longer distances instead of changing to the common species. A high vision therefore increases the frequency dependence and a very low vision shifts the advantage towards the more abundant species.
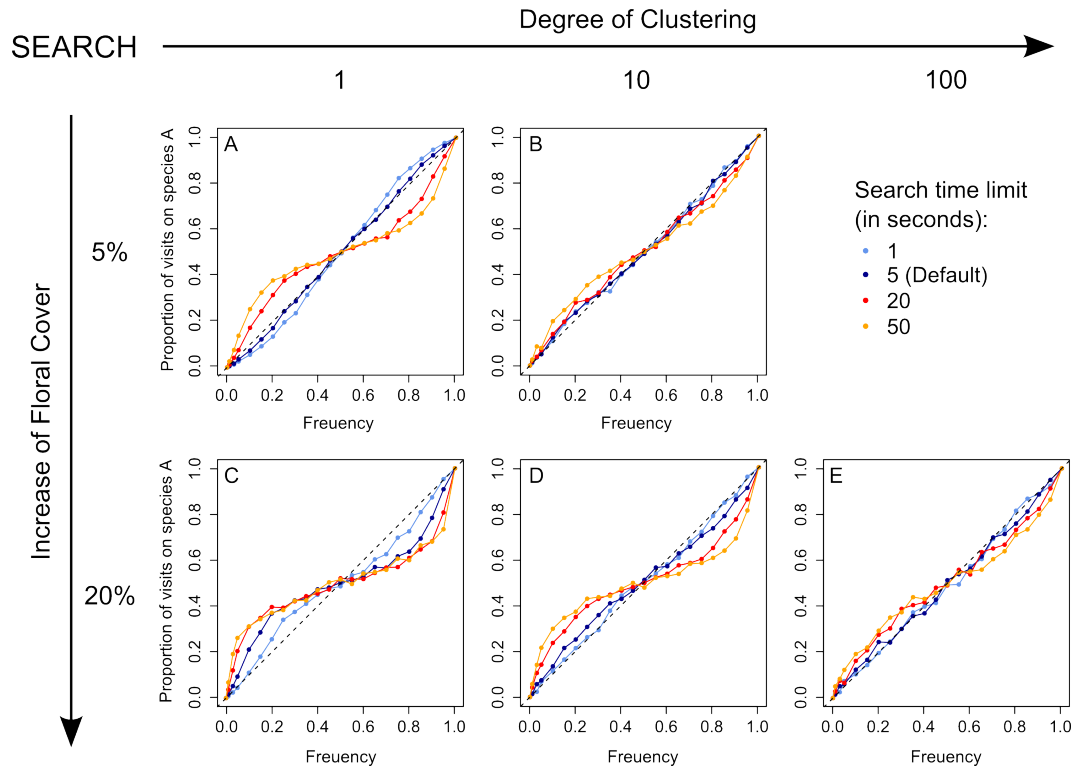
Figure S8: Sensitivity analysis for search limits of 1,5, 20 and 50 seconds. The search limit is the number of seconds within a bee-agent searches for a unvisited and preferred flower, moving around the meadow by a correlated random walk. After the search limit is reached, the probability to change its flower preference increases with every additional second of unsuccessful search. The search limit has a similar effect on the outcome of the model as the vision because it also influences the change probability. With a higher search time, the bee-agent continues searing instead of switching to the more abundant flower, the frequency dependence is increased. A higher cluster value weakens the effect.
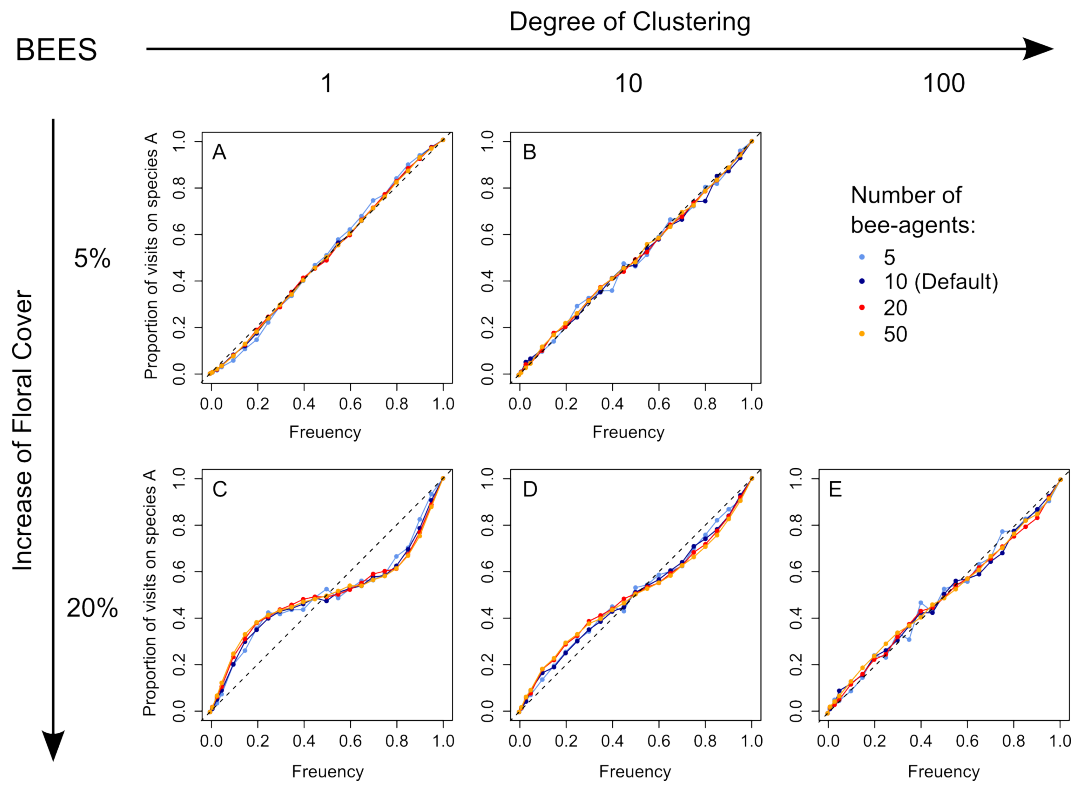
Figure S9: Results of the model for 5, 10, 20 and 50 bee-agents on the meadow. The proportion of visits does not change, only the absolute numbers. Therefore has the pollinator density no influence on the frequency dependence.